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Key role of the amphipod *Gmelinoides fasciatus* in reed beds of Lake Ladoga

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The Baikalian amphipod *Gmelinoides fasciatus*, a successful invader in Eurasia, colonized the coastal zone of Lake Ladoga (northeastern Europe) in late 1990s. In the summers of 2000 and 2005 the density and biomass of benthic communities associated with macrophyte beds (*Phragmites australis*) and role of the invader in fish diet were studied. Due to high production of macrophytes (600–800 g carbon m^{-2} y^{-1}) the benthic biomass was high, averaging 70.6 g m^{-2} in 2005. Whilst the mean benthic biomass showed a 2-fold increase from 1990 to 2005, the biomass of native benthos 2-fold decreased, from 33.6 ± 6.6 to 16.5 ± 6.5 g m^{-2}. *Gmelinoides fasciatus* reached 54 ± 13 g m^{-2} and constituted 77% in the zoobenthic biomass in 2005 as compared with 6% in 1990. Some crustaceans such as *Gammarus lacustris* and *Asellus aquaticus* reduced notably their distribution area and decreased in density. *G. fasciatus* is an important food item in diet of ruffe, perch and young burbot.

Introduction

Invasive species can play important community structuring roles in diverse aquatic ecosystems. They may enter into direct competition with native species through predation, resource competition and modification of habitats, resulting in replacement of vulnerable natives (Elton 1958, Leppäkoski *et al*. 2002). Significant shifts in native communities have been recorded as a consequence of amphipod invasions (Leppäkoski *et al*. 2002, Kelly and Dick 2005, Berezina 2007a, 2007b). The Baikalian amphipod, *Gmelinoides fasciatus* (Stebbing), is one of the most successful invaders in eastern Europe and Siberia. Since the 1970s, it has been established in the Baltic Sea basin including the Neva Estuary, large lakes (Lakes Ladoga, Onega and Peipsi) and most of the small lakes in northwestern and central Russia (Berezina 2007a). In Lake Ladoga, *G. fasciatus* was first found in the late 1980s (Panov 1996). Although it is known to be the most abundant species in all invaded European lakes (Berezina 2007a, 2007b and literature herein), its place in lake food webs is still not clear.

The present study focuses on the state of macroinvertebrate communities associated with macrophyte beds (mainly *Phragmites australis*) in Lake Ladoga in 2000 and 2005 and an evaluation of the role of *G. fasciatus* in these communities and fish diets. The density and biomass of macroinvertebrates was compared with earlier

records in 1990 (after Kurashov *et al*. 1996, Panov 1996) in order to find possible shifts in benthic communities caused by the establishment of a new species.

Materials and methods

Study sites

Lake Ladoga, the largest in the northwestern part of Russia and Europe (18 135 km^2 area, 46.9 m mean depth), has a mesotrophic status but is subject to eutrophication in numerous shallow bays (Filatov and Pozdniakov 2000). The littoral zone, limited by a depth of 8 m, the lower boundary of macrophytes, constitutes 31% of the total lake area (Raspopov *et al*. 1996). Before 1970s Lake Ladoga had had oligotrophic status, then during two decades its ecological status deteriorated catastrophically as a result of anthropogenic pollution (Lozovik *et al*. 2000). Several thousands of enterprises discharged waste waters into the lake and its drainage area. The pulp, chemical and metallurgical mills and agroindustrial complexes are principal sources of pollution in the case of Lake Ladoga (Frumin *et al*. 2000).

In 1980–1990s phosphorus loading to this lake varied from 2300 to 6800 tonnes per year (Kondratyev *et al*. 1998). During 1970–1980, the total phosphorus concentration in water had been 21–26 μg l^{-1} while in the 1990s it did not exceed 17 μg l^{-1} (Modern state … 1998, Filatov and Pozdnyakov 2000). By the year 2000, the state of many polluted locations improved owing to liquidation of some large pulp mills (Filatov and Pozdnyakov 2000, Frumin *et al*. 2000). However, eutrophication process in the lake is still in progress especially in its coastal zone (Andronnikova and Raspopov 2007). "Hot spots" are southern and western coasts of Lake Ladoga including mouths of Rivers Volkhov, Burnaya, Vladimirskij and Shchuchij Bays (near Priozersk city) and some northern locations such as Pitkaranta, Sortavala, Laskela and Lahdenpohja bays (Raspopov *et al*. 1996, Lozovik *et al*. 2000, Luotonen *et al*. 2004, Petrova *et al*. 2005). The Valaam Archipelago, eastern coast and northern skerry areas of the lake are characterized by the most favorable ecological state (Raspopov *et al*. 1996, Petrova *et al*. 2005).

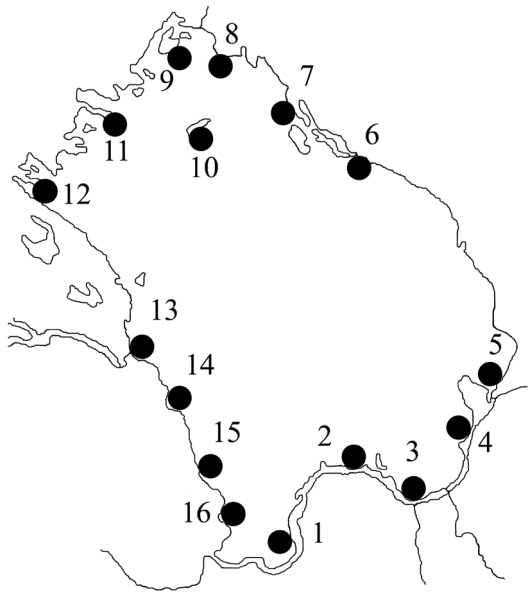

Fig. 1. Sampling sites (1–16) in Lake Ladoga.

We chose 16 study sites in the shallow stone-sandy littoral zone of Lake Ladoga with developed macrophytes, mainly *P. australis* (Fig. 1 and Table 1). Macrophyte and macroinvertebrate communities were studied during 20–31 July 2000 and 5–9 August 2005. All sampling sites (and microhabitats) were the same during both sampling periods, as confirmed by a satellite navigation system (GPS). Geographical coordinates, daytime temperatures and sampling depths at the study sites are listed in Table 1. Bottom sediments were of mixed substrates (stones, gravel and sand). The coverage of hard substrates reached a maximum of 90% at Site 10 and varied between 20% and 60% at all others.

During the study periods, the northern Sites 8, 9 and 11 were not subjected to significant anthropogenic stress. The other sites were exposed to anthropogenic eutrophication and chemical pollution in different degree. The sites 1, 2, 15 and 16 in southern part of the lake were testified as eutrophic areas. The Volkhov Bay (Site 3) was influenced by wastewater discharges from aluminum plant which is situated on the Volkhov River. These discharges are sources of nitrogen and phosphates resulting in eutrophication of the southern part of the lake (Naumenko *et al*. 2000). Also, waste waters from the Syas pulp mills released waste waters to this part of the lake up to 1998 (Frumin *et al*. 2000).

Pollution resulted in a nitrogen to phosphorus ratio of 13–17 indicating hyper-eutrophic conditions (Frumin *et al*. 2000). Besides, the Volkhov and Svir Bays (Site 4) take humic waters from wetlands and bogs. The amounts of humic compounds contribute 65%–92% to the total organic carbon in waters of the Volkhov River (Korkishko *et al*. 2000). Humic compounds can be an important source of nutrients and microelements facilitating further eutrophication of the lake (Korkishko *et al*. 2000). The Shchuchij Bay (Site 12) and tens of kilometers of lake area to the south from it were heavily polluted up to the 1980s because of intensive waste water discharges from a pulp mill (Slepukhina *et al*. 2000). During the study years, the Shchuchij Bay retained properties of an eutrophic area with intensive macrophyte beds. Moreover, high contents of technogenic materials (to 70%) were recorded in sediments of the bay. Waters of the Vladimirovskij Bay (Site 14) were influenced by moderate oil pollution in both 2000 and 2005. Earlier it had also been characterized as eutrophied and polluted area (Raspopov *et al*. 1996).

Sampling and laboratory procedures

Macrophyte communities were described according to Katanskaya (1981). The projective area coverage of species in beds was estimated visually. The sampling frames with areas of 0.125 m^2 (3 replicates) and 0.03 m^2 (5 replicates) were used for collecting quantitative samples of macrophytes. To measure height and biomass of *P. australis*, 7–30 shoots of flowering plants (depending on the heterogeneity of the bed) were randomly sampled. Prior to weighing, macrophytes were rinsed in tap water and dried at 60 °C for 96 hours. Annual primary macrophyte production (PP, g carbon (C) m^{-2}) was estimated as a function of the maximal elevated biomass of plants (B_{max}, g C m^{-2}): PP = $1.2B_{max}$ (Raspopov 1985).

Quantitative samples of macroinvertebrates were obtained with a 0.03-m^2 diameter cylindrical metal frame (0.76 m height), with three replicates taken at each site. The frame was forced into the bottom and all the hard substrates and plants in the frame were transferred to a plastic container filled with fresh water. Animals were washed off the hard substrates or scraped off with a knife (for attached animals). A 3–7 cm layer of soft sediments was collected with a hand-held net (0.25 mm mesh size) for three minutes. All parts of the sample were placed in a sieve (0.25 mm), rinsed with water, transferred to a plastic zip-bag and preserved in 4% formaldehyde.

Table 1. Coordinates, sampling depths and daytime temperature of water at study sites.

Site	Lat. N	Long. E	Water depth (m)		Temperature (°C)	
			2000	2005	2000	2005
1	60°01′04″	31°32′39″	0.65	0.7	20	20
2	60°13′17″	31°55′36″	0.6	0.6	21	20
3	60°07′52″	32°19′26″	0.65	0.75	21	19.5
4	60°31′26″	32°41′13″	0.4	0.7	21	20
5	60°58′45″	32°36′26″	0.6	0.7	19.5	20
6	61°20′30″	31°39′51″	0.45	0.5	19	20
7	61°24′03″	31°30′31″	0.6	0.6	21	19
8	61°37′16″	31°10′35″	0.6	0.5	20	19
9	61°38′07″	31°11′26″	0.5	0.7	21	19.5
10	61°21′35″	30°53′18″	0.2	0.5	18	18
11	61°31′07″	30°33′27″	0.5	0.6	17	17.5
12	61°04′59″	30°05′22″	0.3	0.6	17	18
13	60°50′10″	30°28′06″	0.5	0.7	17	19
14	60°37′05″	30°31′59″	0.3	0.6	17	18
15	60°22′46″	30°52′48″	0.5	0.7	18	17
16	60°06′39″	31°05′29″	0.4	0.7	17.5	19

In the laboratory, the samples were analyzed under a stereoscopic microscope (16×). All the invertebrates were sorted into 13 groups (taxa): Oligochaeta, Hirudinea, Planaria, Gastropoda, Bivalvia, Amphipoda, Isopoda, Chironomidae, Coleoptera, Ephemeroptera, Odonata, Trichoptera and others. To determine wet weights, animals were blotted with filter paper to remove surface water and weighed on a torsion balance (± 0.01 mg). The relative density (or biomass) of each taxon was calculated as its percentage of the total density (or biomass).

The diets of three species of fish, the burbot *Lota lota*, perch *Perca fluviatilis* and ruffe *Gymnocephalus cernuus*, were analyzed quantitatively. In 2005, fish were collected with a gill net (for 4–5 hours) from the littoral zone in the southern (near Site 2) and northern (Site 9) parts of Lake Ladoga. Previous visual examinations of stomach contents of other fish, including the roach *Rutilus rutilus*, rudd *Scardinius erythrophthalmus*, smelt *Osmerus eperlanus* and vendace *Coregonus albula*, had shown that *G. fasciatus* was not included in their diet.

A stomach was excised from the body cavity using needles, tweezers and scalpel and transferred to a Petri dish. The fullness of the stomach was approximated using a 0%–100% scale, with 0% indicating an empty cavity and 100% denoting a very full one. We analyzed only stomachs with 80%–100% fullness: 16 from the perch with body lengths 11–18 cm, 18 from the ruffe (7–15 cm) and 10 from the burbot (10–18 cm) from each location. All the food items were identified under a microscope and weighed. The percentage wet mass of each food item in the entire stomach content was calculated.

All characteristics were expressed as arithmetic means ± standard errors (SE). The structural characteristics of macrophytes and macroinvertebrates were log-normalized and examined with respect to sites and years using ANOVA, with Fisher's protected least significant difference post-hoc test (*F*-test). Data on the biomasses of zoobenthic taxa were grouped between sites using hierarchical clustering using the weighted pair-group method. The arcsine-transformed proportions of food items were analyzed using ANOVA and the *F*-test with respect to item type. Differences between two sites in the proportions of food items for each species of fish were examined with a paired *t*-test.

Results

Macrophytes

The helophyte *P. australis* was the most abundant species in macrophyte beds at all study sites except Site 10, which was dominated by submerged hydrophytes (75% coverage, mainly *Potamogeton perfoliatus* and *P. gramineus*). Coverage of *P. australis* in beds varied from 50% to 100%, with an average of 79.2% ± 3.9% in 2000 and 75.5% ± 3.5% in 2005. The differences between years were not significant ($F_{1,30} = 0.47$, $p > 0.05$). However, coverage of *P. australis* was significantly different between sites ($F_{1,30} = 2.7$, $p < 0.05$), reaching a maximum (80%–100%) in the southern part of Lake Ladoga in both years (Sites 1–5 and 16).

Significant differences between years in the height ($F_{1,30} = 7.8$, $p < 0.01$) and density ($F_{1,30} = 18.7$, $p < 0.001$) of *P. australis* beds were recorded. The average density of these beds was significantly (1.8×) greater in 2005 than in 2000 (158 ± 14 ind. m^{-2} and 87 ± 11 ind. m^{-2}, respectively, $t = 4.52$, $p < 0.001$). In contrast, their average height was significantly ($p < 0.01$) smaller in 2005 (1.5 ± 0.1 m) than in 2000 (2.0 ± 0.1 m).

Coverage of *P. gramineus* and *P. perfoliatus* in *P. australis* beds was not high at most sites and reached 20%–30% at Sites 9, 11 and 13. The macrophytes *Eleocharis palustris*, *Zannichellia palustris* and *Potamogeton* spp., which were found with low density at most sites, covered a maximum of 30% at Site 12. *Elodea canadensis* was recorded in small numbers in bays of the western coast (Sites 11–14).

The annual production of *P. australis* averaged 606 ± 80 g C m^{-2}, with maxima (960–1100 g C m^{-2}) at Sites 2 and 5. The primary production of *P. gramineus* (11–27 g C m^{-2} per year) was almost 2-fold lower than primary production of *P. perfoliatus* (27–62 g C m^{-2} per year). The production of other macrophytes averaged 24 ± 10 g C m^{-2} per year. The total annual production of macrophyte beds in the littoral zone studied reached 688 ± 108 g C m^{-2}.

Macroinvertebrates

Significant differences in biomass and density of benthos between sites were revealed in both years (all $p < 0.001$, Table 2). The benthos was most abundant in the southern part of the lake, both in 2000 (Site 2, 63 400 ind. m^{-2} and 155 g m^{-2}) and 2005 (Site 15, 79 200 ind. m^{-2} and 200 g m^{-2}). There were significant differences between sites in the relative biomass of oligochaetes, chironomids, the amphipod *G. fasciatus* and other benthic groups in both 2000 and 2005 (all $p < 0.001$, Fig. 2).

Cluster analysis revealed that in 2000 there were five groups of communities differing in the biomass of benthos and the contributions of different taxa to the biomass (Fig. 3). The total biomass and the biomass of *G. fasciatus*, which constituted 89%–97%, were similarly high (56–64 g m^{-2}) in the northwestern part (Sites 12, 13) and near the Valaam Island (Site 10, Table 2, Fig. 3). The biomass of benthos exceeded 30 g m^{-2} at Sites 1 and 16 (southern coast), where *G. fasciatus* constituted 84% and 99% of the total. At Sites 5, 6, 8, 14 and 15, benthic biomass reached 20–32 g m^{-2} and the contribution of *G. fasciatus* was 41%–97.5% of the total. Benthic communities in the Svir Bay (Site 3) and Volkhov Bay (Site 4) and in the northern Sites 7, 9 and 11 were not abundant, ranging from 2 to 8 g m^{-2}. The oligochaetes, chironomids and other insects composed 52%–98% of the total biomass at these sites, while the invasive amphipod was either not found or rare. The highest biomass of *G. fasciatus* (149.5 g m^{-2}, 96%) was recorded at Site 2 on the southern coast of the lake.

In 2005, *G. fasciatus* was found at all sites. Cluster analysis showed that the distribution of the biomass among invertebrate taxa at different sites was highly heterogeneous (Fig. 4). The highest biomass of *G. fasciatus* (162 g m^{-2} and 68.4%) was recorded at the southern Site 15. The total biomass was above 100 g m^{-2} at Sites 2 and 6, where the relative biomass of Baikalian amphipods reached 93%–94% (Table 2). *G. fasciatus* was abundant at Sites 8, 14 and 16 (72–80 g m^{-2}), contributing 76%–92% of the total biomass. The biomass of *G. fasciatus* was significantly lower at Sites 10 and 12 (24 and 28 g m^{-2}, 57% and 65%). The lowest benthic biomasses were recorded at Sites 3 (4.3 g m^{-2}) and 4 (9.4 g m^{-2}). These sites and the northern Sites 7 and 9 were dominated by chironomids and oligochaetes (more than 40%) and the proportion of

Table 2. Absolute mean (± SE) density (*N*, thousands ind. m^{-2}) and biomass (*B*, g m^{-2}) of macrozoobenthos and relative (%) density (N_G, %) and biomass (B_G, %) of *Gmelinoides fasciatus* at study sites.

Site	Macrozoobenthos				*G. fasciatus*			
	N		*B*		N_G		B_G	
	2000	2005	2000	2005	2000	2005	2000	2005
1	14.8 ± 1.2	16.0 ± 1.2	30.9 ± 1.7	16.5 ± 2.6	83.8	84.9	84.3	79.4
2	63.4 ± 9.8	64.9 ± 10.3	155.3 ± 56.1	116.7 ± 12.3	94.0	94.6	96.3	93.8
3	7.5 ± 5.0	6.5 ± 1.1	5.4 ± 1.1	4.3 ± 0.3	8.3	7.1	48.4	22.2
4	9.1 ± 0.5	5.0 ± 1.5	5.7 ± 0.2	9.4 ± 2.2	0.7	0.4	0.2	3.2
5	12.6 ± 0.9	38.5 ± 19.9	28.6 ± 10.0	100.5 ± 72.3	54.5	94.9	40.8	78.1
6	11.5 ± 5.8	57.1 ± 13.3	22.9 ± 13.3	139.3 ± 23.2	86.5	92.2	97.5	93.3
7	3.7 ± 0.1	19.1 ± 1.8	2.4 ± 0.2	26.2 ± 15.3	1.7	0.7	21.2	1.0
8	26.3 ± 4.0	38.4 ± 10.0	19.8 ± 4.0	96.5 ± 21.3	50.9	83.1	78.3	75.8
9	14.8 ± 8.0	17.2 ± 2.5	8.3 ± 4.0	50.9 ± 20.4	24.3	24.1	52.9	24.2
10	54.1 ± 12.0	16.4 ± 8.2	56.3 ± 13.0	44.7 ± 21.7	69.1	63.9	88.8	64.9
11	15.9 ± 4.0	24.7 ± 4.0	5.5 ± 0.2	66.0 ± 11.6	0	77.4	0	86.9
12	27.5 ± 2.5	30.4 ± 6.6	63.9 ± 11.6	43.9 ± 18.5	71.6	56.3	89.3	56.9
13	26.5 ± 4.0	5.2 ± 2.2	57.5 ± 23.2	34.6 ± 14.4	88.6	25.3	96.8	22.8
14	17.1 ± 1.8	66.4 ± 12.4	20.5 ± 1.8	94.7 ± 49.4	58.2	92.0	90.1	85.8
15	10.0 ± 6.9	79.2 ± 6.4	31.6 ± 6.9	200.0 ± 106.2	47.9	64.7	71.6	68.4
16	12.7 ± 3.4	33.6 ± 7.8	39.4 ± 10.0	79.7 ± 21.2	83.8	94.7	99.0	92.1

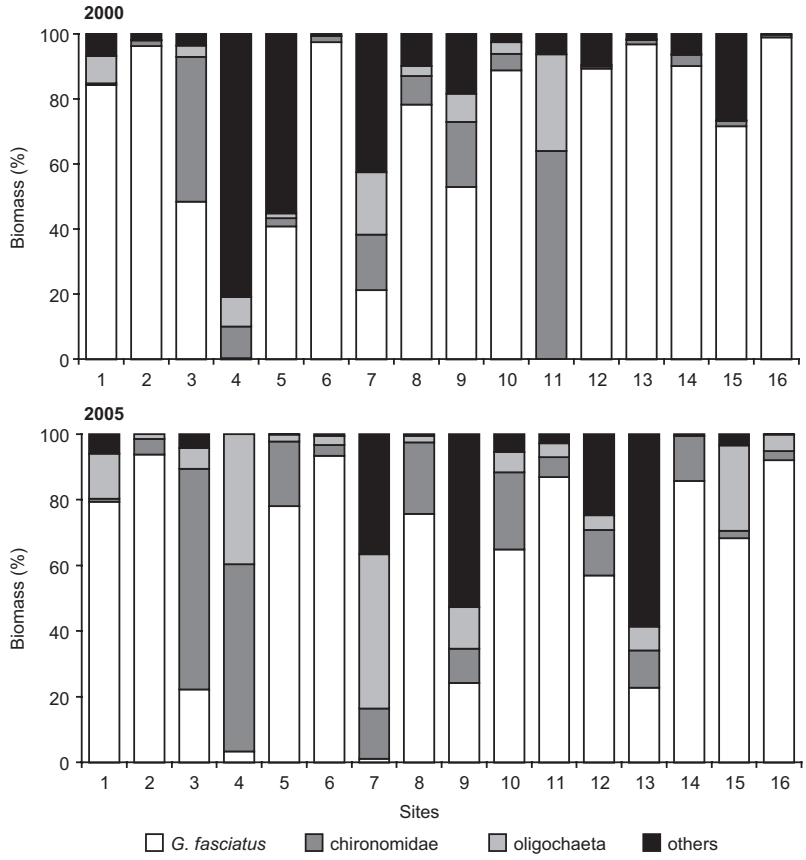

Fig. 2. Relative biomass (%) of *Gmelinoides fasciatus*, chironomids, oligochaetes and other benthic taxa at the study sites in 2000 and 2005.

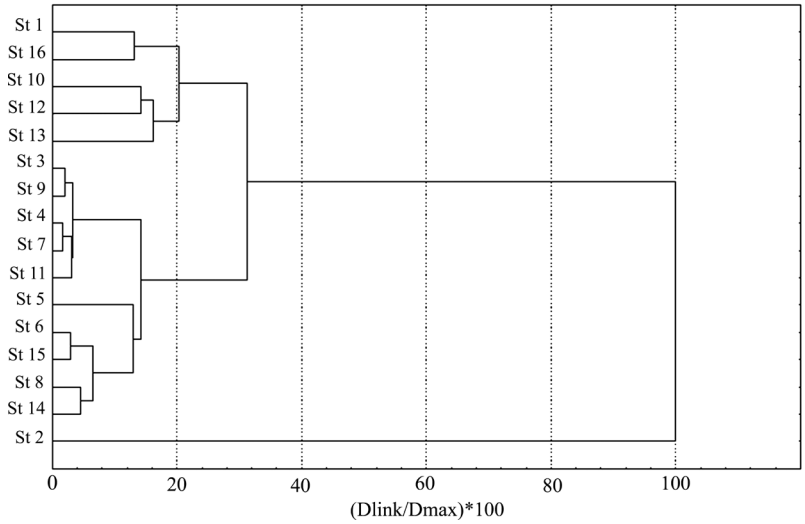

Fig. 3. Similarity of study sites in Lake Ladoga (2000) as regards macroinvertebrate biomas (Oligochaeta, Hirudinea, Planaria, Gastropoda, Bivalvia, Gmelinoides, Isopoda, Chironomidae, Coleoptera, Trichoptera, Ephemeroptera, Odonata and others). Dendrogram for hierarchical clustering of the 16 sites, using weighted pair-group method calculated on log-transformed data.

G. fasciatus in the community was low (Table 2 and Fig. 4).

Significant differences between the years were found in the average biomass ($F_{12,195} = 16.3$, $p < 0.0001$) and the density ($F_{12,195} = 17.1$, $p < 0.0001$) of benthic groups. The average biomass of *G. fasciatus* was significantly ($p < 0.05$) higher in 2005 (54 g m^{-2}) than in 2000 (24.7 g m^{-2}, Fig.

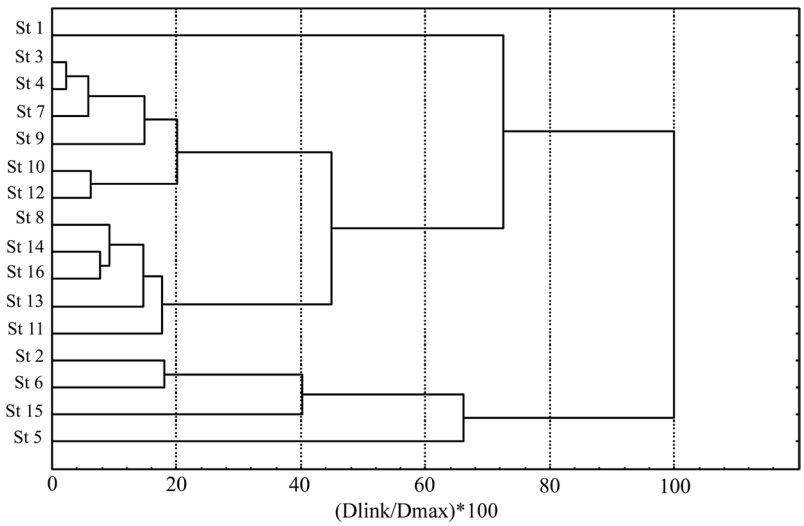

Fig. 4. Similarity of study sites in Lake Ladoga (2005) as regards macroinvertebrate biomass (Oligochaeta, Hirudinea, Planaria, Gastropoda, Bivalvia, Gmelinoides, Isopoda, Chironomidae, Coleoptera, Trichoptera, Ephemeroptera, Odonata and others). Dendrogram for hierarchical clustering of the 16 sites, using weighted pair-group method calculated on log -transformed data.

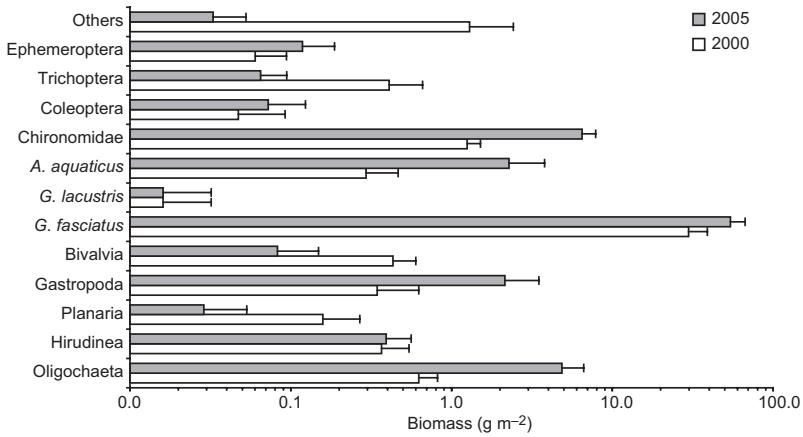

Fig. 5. Biomass (mean + SE, g m^{-2}) of benthic taxa in littoral zone of Lake Ladoga, associated with *Phragmites australis* beds in 2000 and 2005.

5). Also, the average biomasses of chironomids and oligochaetes were significantly (all $p < 0.01$) higher in 2005 than in 2000. In 2000, the isopod *Asellus aquaticus* was recorded at most sites but was not abundant (0.5 g m^{-2}). In 2005, it was not found at the southern and eastern Sites 1–5 and 16, but locally reached high biomass (18 g m^{-2} at Site 9, 6.9 g m^{-2} at Site 12 and 3.7 g m^{-2} at Site 15). The other amphipod, *Gammarus lacustris*, was rare. It was recorded at Sites 3, 9 and 10 in 2000 but only at Site 9 in 2005.

Comparison of the benthos characteristics in *P. australis* beds with the data from 1990 showed that there has been an abrupt change in the biomass and density proportions of the main taxa (Fig. 6). The total biomasses of benthos in this biotope in 1990 (33.8 g m^{-2}, Kurashov *et al*. 1996) and 2000 (34.6 g m^{-2}) were very simi-

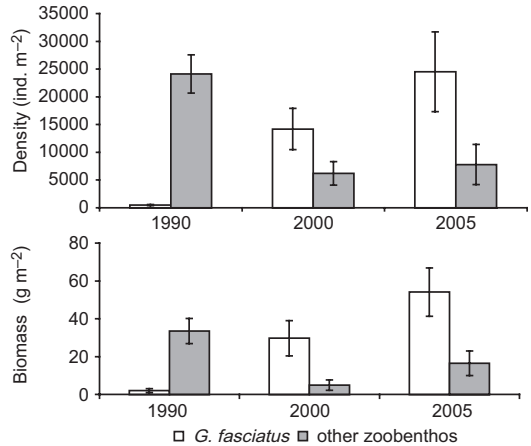

Fig. 6. Summer biomass (mean ± SE, g m^{-2}) and density (mean ± SE, ind. m^{-2}) of *Gmelinoides fasciatus* and other macroinvertebrates in *Phragmites australis* beds in 1990 (from Kurashov *et al.* 1996 and Panov 1996) 2000 and 2005.

lar, but the contribution of the native benthos decreased from 99% to 14%. The total biomass and density of the benthic community increased further during 2000–2005 as a result of an increased abundance of *G. fasciatus* and other benthic groups (Fig. 6). The average contribution of *G. fasciatus* to the total density and biomass of littoral benthos exceeded 70% in both 2000 and 2005. For 15 years (1990–2005) the density and biomass of the new species increased markedly whereas the density of the native benthic community decreased at least 3-fold and its biomass 2-fold.

Fish diet

There were significant differences in the contributions of different food items to the stomach contents of the fishes studied ($F_{13,70}$ = 3.14, p < 0.001, Table 3). Amphipods constituted the main mass proportions in the diets of the perch (63.5%–66.7%), ruffe (68.1%–87.3%) and burbot (61.1%–76.4%). The role of *G. fasciatus* in fish diets varied significantly between sites (perch: t_{15} = 6.17, p < 0.001, ruffe: t_{17} = 37.5, p < 0.0001 and burbot: t_9 = 17.6, p < 0.0001). *Gmelinoides fasciatus* was the main item in the diet of the burbot (76.4%), perch (63.5%) and ruffe (87.3%) in the southern part of the lake (Site 2), while it constituted 3%–4% of the diet of perch and ruffe in the northern location (Site 9). The taxonomic compositions of fish diets were more diverse in the northern than the southern location (Table 3). The native amphipod *Monoporeia affinis* dominated (62%) in the diets of perch and ruffe, and another native amphipod, *Pallasea quadrispinosa*, constituted 57% of the diet of burbot.

Discussion

Differences in the structure and productivity of *P. australis* beds among sites in Lake Ladoga were caused by the varied trophic status of the coastal zone. The highest production was recorded in the more eutrophic southern part of the lake. The density of the reed beds was significantly higher in 2005 than in 2000 or in the 1960s (Raspopov 1985 and literature therein), perhaps testifying to an intensive expansion of reeds as a result of increasing lake eutrophication. It was shown that expansion of *P. australis* in Lake Peipsi, and the subsequent decrease of open areas, resulted in a decline of the species richness of macrophytes in the shallowest zone (Mäemets and Freiberg 2004). A local decrease in community diversity may facilitate introductions of invasive species according the proposition (Elton 1958) that communities with greater species richness are more

Table 3. Mean (± SE) mass proportion (%) of diverse food items in stomach contents of perch *Perca fluviatilis*, ruffe *Gymnocephalus cernuus* and burbot *Lota lota* from two sites in the littoral zone of Lake Ladoga.

Food item	*P. fluviatilis*		*G. cernuus*		*L. lota*	
	Site 2	Site 9	Site 2	Site 9	Site 2	Site 9
Gmelinoides fasciatus	63.5±0.1	3.2±2.1	87.3±1.4	4.0±1.5	76.4±4.5	–
Monoporeia affinis	–	62.5±8.6	–	62.4±5.4	–	–
Pallasea quadrispinosa	–	1.0±0.7	–	1.7±0.7	–	57.3±5.8
Asellus aquaticus	–	–	–	–	–	3.8±0.9
Mysidacea	–	–	–	0.5±0.5	–	–
Oligochaeta	–	–	5.5±1.7	0.5±0.5	0.1±0.01	0.5±0.2
Hirudinea	–	–	–	3.3±2.2	–	0.3±0.1
Bivalvia (Pisidiidae)	–	–	–	–	–	1.0±0.6
Chironomidae	3.9±2.0	4.0±1.5	1.3±0.6	20.0±4.6	2.4±0.05	7.1±3.3
Trichoptera	2±1.4	1.3±0.7	4.9±1.3	5.9±2.1	4.0±0.9	5.8±2.0
Coleoptera	–	–	–	1.0±0.6	3.1±0.81	0.2±0.05
Ephemeroptera	–	–	1.0±0.5	–	–	–
Ceratopogonidae	–	–	–	1.9±1.9	–	–
Fish	30.6±10	30.8±9.6	–	–	14.5±8.0	38.5±8.0

stable and therefore less vulnerable to invasion. It is worth mentioning that *E. canadensis* is extending its distribution in Lake Ladoga (Raspopov *et al*. 1996, Zhakova 2004).

No changes in the number of malacostracan species in Lake Ladoga have occurred since the middle of the 20th century (Gordeev 1965, Stalmakova 1968), apart from the addition of the Baikalian amphipod. At present, *Gammaracanthus lacustris*, *Gammarus lacustris*, *G. fasciatus*, *M. affinis*, *P. quadrispinosa*, *A. aquaticus*, *Saduria entomon* and *Mysis* spp. inhabit different zones of this lake. According to Audzijonyte and Väinölä (2005), two sympatric species *Mysis relicta* and *M. salemaai* can inhabit Lake Ladoga, but this question warrants further clarifications. However, abrupt changes were recorded in the quantitative roles of some of them. The newcomer *G. fasciatus*, became very abundant in the coastal zone of Lake Ladoga. Its mean biomass reached 54 ± 13 g m^{-2} with a maximum of 162 g m^{-2} in 2005. It constitutes more than 70% of the total biomass and density of macroinvertebrates in *P. australis* beds. Similar population size of *G. fasciatus* (79%–93% of the benthos) was found in 2002 at exposed littoral sites along the Valaam Island (Kurashov *et al*. 2006).

The large population size of *G. fasciatus* in Lake Ladoga is a result of the high reproductive potential and environmental tolerance of this amphipod species (Berezina 2007a, 2007b). The expanded distribution and increase in density of the reed beds also result in an increase in the area of microhabitats (roots and debris) for amphipods and their abundance per unit of bottom area. Extensive *P. australis* beds produce large amounts of organic matter (up to 1100 g *C* m^{-2} per year), which are unlimited food resources for detritivorous invertebrates as *G. fasciatus*.

The increase in biomass of all invertebrate groups in 2005 compared with that in 2000 may also indirectly confirm the eutrophication in the littoral zone of Lake Ladoga. Increase in macrobenthic biomass was noted in different areas of the lake from 1960 to 1980–1990s (Slepukhina *et al*. 2000). Similarly, increase in quantity and some changes in structure of meiobenthos were recorded since 1980s to 1998–2004 (Kurashov 2005). Inorganic phosphorus concentrations in water were ten times higher in 1990s than in the beginning 1960s (Filatov 2000), that also testifies to eutrophication process in the lake. Oligochaetes (*Potamothrix hammoniensis*, *Limnodrilus* sp.) became common components of the macrofauna from 1980s, indicating eutrophic conditions in deepwater areas (Slephukhina *et al*. 2000). Besides, meiobenthic species (*Cyclops* spp.) with α-mezo-saprobic indicatory significance were recorded in some locations of the lake (Kurashov 2005).

Gmelinoides fasciatus has many trophic links with other invertebrates through predation. Although specimens with body lengths of up to 7 mm preferentially consume detritus (70%–90% of the diet), the larger specimens are predaceous omnivores with about 35% of animal food in their diets (Berezina *et al*. 2005). Local disappearances of *Gammarus lacustris* and *A. aquaticus* may be a result of antagonistic relationships (predation and competition) between these species and *G. fasciatus*. For example, in the 1960s, *G. lacustris* inhabited macrophyte beds and exposed stones along the entire shore of Lake Ladoga (Kuzmenko 1964). When the *G. fasciatus* expansion began (late 1980s), native *G. lacustris* constituted 90% of the total density (890 ind. m^{-2}) and and 84.5% of the total biomass (1.65 g m^{-2}) of amphipods in *P. australis* beds, while the newcomer accounted for less than 10% (Kurashov *et al*. 1996). By 2005, native *G. lacustris* had become a very rare species. The isopod *A. aquaticus* reached high abundances only at sites with low *G. fasciatus* density, since it is under predation pressure by *G. fasciatus*. Similarly, a decrease in *A. aquaticus* density after establishment of the amphipod *Pontogammarus robustoides* has been confirmed in some Lithuanian lakes (Arbačiauskas 2005). Likewise, the predaceous omnivore *Gammarus pulex* dramatically altered the macroinvertebrate and fish communities in Irish waters through strong predation (Kelly and Dick 2005).

Gmelinoides fasciatus is tolerant to water polluted by oil, pulp-mill discharges and hard eutrophication (Lake Ladoga 2000, Berezina 2007a and literature therein). Nevertheless, it was rare in the Volkhov Bay, which is influenced by wastewaters from an aluminum plant. Similarly, local disappearance of the previously common amphipods *P. quadrispinosa* and *M.*

affinis due to pollution was recorded in this bay in 1970–1980s (Naumenko *et al*. 2000).

Extremely low frequency of *Gmelinoides fasciatus* was recorded in the Svir Bay, where the water is enriched by humic compounds. Humification is known as a factor influencing negatively on distribution of amphipods in lakes (Gordeev 1965). For example, being common species in oligotrophic and mesotrophic lakes, the amphipods *Gammarus lacustris*, *P. quadrispinosa* and *M. affinis* were never found in dystrophic lakes with humified waters in Karelian region (Gordeev 1965).

The Baikalian amphipod *G. fasciatus* was introduced into different aquatic ecosystems of the former USSR with the aim of enhancing food base for fish (Berezina 2007a). It has become a regular but not abundant item in the diets of the bream *Abramis brama*, the ide *Leuciscus idus*, the pikeperch *Sander lucioperca*, the roach and the burbot in lakes of northwestern Russia and Siberia, while it is known as a main food item (more than 65%) in the diet of perch (Mitskevich 1981, Berezina 2007a and literature therein). In Lake Ladoga, *G. fasciatus* was included in the diets of ruffe, young burbot and perch; its proportions in these diets depended on its abundance in the natural habitats. At northern locations, where *G. fasciatus* was not abundant, fish foraged mainly on native amphipods (*P. quadrispinosa* and *M. affinis*) and chironomids.

Although the invasive amphipod *G. fasciatus* has become established in Lake Ladoga recently, this study has documented its high population size and key role in littoral benthic communities. The invasion of this species was accompanied by alterations in the community structures and a decrease in the absolute biomass and percentage of native macroinvertebrates. A more detailed assessment of all trophic links is needed to determine the influence of *G. fasciatus* on the lake ecosystem.

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